Data gaps and opportunities for comparative and conservation biology

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Biodiversity loss is a major challenge. Over the past century, the average rate of vertebrate extinction has been about 100-fold higher than the estimated background rate and population declines continue to increase globally. Birth and death rates determine the pace of population increase or decline, thus driving the expansion or extinction of a species. Design of species conservation policies hence depends on demographic data (e.g., for extinction risk assessments or estimation of harvesting quotas). However, an overview of the accessible data, even for better known taxa, is lacking. Here, we present the Demographic Species Knowledge Index, which classifies the available information for 32,144 (97%) of extant described mammals, birds, reptiles, and amphibians. We show that only 1.3% of the tetrapod species have comprehensive information on birth and death rates. We found no demographic measures, not even crude ones such as maximum life span or typical litter/clutch size, for 65% of threatened tetrapods. More field studies are needed; however, some progress can be made by digitalizing existing knowledge, by imputing data from related species with similar life histories, and by using information from captive populations. We show that data from zoos and aquariums in the Species360 network can significantly improve knowledge for an almost eightfold gain. Assessing the landscape of limited demographic knowledge is essential to prioritize ways to fill data gaps. Such information is urgently needed to implement management strategies to conserve at-risk taxa and to discover new unifying concepts and evolutionary relationships across thousands of tetrapod species.

biodemography | mortality | fertility | extinction | Demographic Species Knowledge Index

Accessible data are increasingly becoming more valuable in research and for decision-making processes worldwide, including conservation. Most of the world's digitally available information has been compiled in the past few years, and data acquisition rates are accelerating (1). Collection and digitization of existing biodiversity data are essential for making more species information available to support conservation actions. Identifying knowledge gaps and catalyzing efforts to generate and use existing information have become priorities for international bodies concerned about the protection of global biodiversity [e.g., the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (2)]. Furthermore, making these data available to scientists and practitioners is important

Significance

Given the current species extinction rates, evidence-based policies to conserve at-risk species are urgently needed. Ultimately, the extinction of a species is determined by birth and death rates, which drive populations to increase or decline. Therefore, demographic data are essential to inform species conservation policies or to develop extinction risk assessments. Demographic information provides an indispensable bedrock for insights to tackle species sustainable management and deepens understanding of ecological and evolutionary processes. We develop a Demographic Species Knowledge Index that classifies the demographic information for 32,144 tetrapod species. We found comprehensive information on birth and survival for only 1.3% (613) of the species, and show the major potential of zoos and aquariums to significantly increase our demographic knowledge.

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Data deposition: Data to perform the analyses have been deposited in the Species360 Open Data Portal with additional figures (https://www.species360.org/serving-conservation/species-knowledge-index/) and in the Dryad Digital Repository (https://doi.org/10.5061/dryad.nq02fm3).

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for international bodies aiming to conserve biodiversity [i.e., Aichi Target 19, Convention on Biological Diversity (3)]. Despite the rapid growth in biodiversity information and data repositories (4), we still do not have a species knowledge index that indicates the types of information available, such as demography, even for the most well-known taxa.

Two decades ago, Carey and Judge (5) pioneered the first major database of demographic diversity across species: They compiled maximum life spans for more than 3,000 vertebrates. Since then, various databases with fertility and mortality information have been launched, including the 22 listed in Table 1. These databases have been used for comparative analyses (6, 7). They can also be used for studies of species conservation. Thus, for both uses, it is important to standardize and integrate knowledge from various sources to get an overall view of available information. Up until our analysis, however, a map was lacking of the landscape of knowledge across species to summarize which taxa have the least information and which have the most.

Digitized demographic data are becoming increasingly available, including characteristics of species such as maximum recorded life span, age at maturity, and litter/clutch size. This is also true for population-level data, including life tables and matrix models, which provide information for populations of individuals about fertility and survival over the ages or stages of life. Although such data repositories have been used for comparative analyses, their combined potential could be improved if inconsistencies in data standards and terminology were resolved (8), thus permitting cross-taxa studies by drawing information from multiple databases.

We developed the Demographic Species Knowledge Index based on a metadatabase analysis of 22 available data repositories (Table 1) on life history traits and demographic data. For 97% of the described tetrapods (9), we were able to obtain some demographic data or determine that no data were available. The index summarizes the existing level of demographic information available for each species. Species with the highest values have information on both survival and fertility across ages or stages (i.e., life tables, population matrices). Low values are obtained when only summary species-level demographic measures are available, such as age at first reproduction or maximum recorded life span. We use the index to map the distribution of survival and fertility knowledge, to highlight current gaps, and to point out directions for future research.

Given the current extinction trends (10) there is a pressing need to develop recovery strategies for threatened species, which heavily depends on demographic data. Deep understanding of population dynamics is required for calculation of generation length or for performing population viability analysis to assess species extinction risk. We found that age- or stage-specific birth and death rates are available for only 1.3% of tetrapods (Figs. 1 and 2 and *SI Appendix*, Figs. S1–S4). For threatened species, this level of information covers a mere 4.4% of the 1,079 threatened mammals, 3.5% of the 1,183 threatened birds, 0.9% of 1,160 threatened reptiles, and 0.2% of the 1,714 threatened amphibians (Table 2 and *SI Appendix*, Tables S1 and S2).

Although life tables or matrix population models are available for only a few species, a range of valuable comparative analyses can be carried out using less detailed information. The most commonly available demographic measure across tetrapods is litter/clutch size, which we found for 11% of amphibians and 64% of birds, followed by maximum recorded life span, which is available for less than 4% of amphibians but for 46% of mammals (Table 3). Knowledge gaps are extensive, especially for amphibians, where 88% of species have no available information, followed by reptiles, with 65% lacking any demographic information (Fig. 1 and *SI Appendix*, Figs. S1–S4).

This deficiency of data is of particular concern since the data are needed for species threat assessments and to establish harvesting quotas. Population reduction, often measured on the scale of generation length, is one of the most important criteria for listing species under different levels of threat by the International Union

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Table 1. Number of species with demographic records in each of the 22 databases compiled for the Demographic Species Knowledge Index

Database (Ref.)	Reptilia	Mammalia	Aves	Amphibia	Total
ALHDB (26)	2,759	3,114	4,931	—	10,804
AnAge (27)	488	1,223	1,105	160	2,976
Biddaba (28)	—	—	777	—	777
BTO (29)	—	—	254	—	254
COMADRE Animal Matrix Database (30)	37	97	73	10	217
DATLife (31)	123	488	654	32	1,297
EDB (32)	—	—	314	—	314
GARD (33–35)	2,127	—	—	—	2,127
Clutch size frogs (36)	—	—	—	470	470
LHTDB of European reptile species (37)	109	—	—	—	109
Clutch size of anurans (38)	—	—	—	385	385
Clutch size of birds (39)	—	—	5,258	—	5,258
Life tables of mammals (16)	—	143	—	—	143
Mean age of anurans (40)	—	—	—	30	30
PanTHERIA (41)	—	2,572	—	—	2,572
PLHD (21)	—	7	—	—	7
Age at sexual maturity and survival of snakes and lizards (42)	30	—	—	—	30
Age at sexual maturity, survival, and mortality rate of turtles (43)	18	—	—	—	18
Clutch size of crocodiles (44)	22	—	—	—	22
Clutch size of lizards (45)	48	—	—	—	48
Database of life-history traits of European amphibians (46)	—	—	—	71	71
Sexual maturity, mean age, and longevity of amphibians (47)	—	—	—	114	114

ALHDB, Amniote Life History Database; AnAge, The Animal Aging and Longevity Database; Biddaba, Bird Demographic Database; BTO, British Trust for Ornithology; DATLife, The Demography of Aging Across the Tree of Life Database; EDB, EURING databank; GARD, Global Assessment of Reptile Distributions; LHTDB, Life History Trait Database; PLHD, Primate Life History Database. Note that DATLife, AnAge, and PanTHERIA include information on maximum observed life spans for thousands of species from a database compiled by James R. Carey and Debra S. Judge, the first major digitalized demographic database for vertebrates (5).

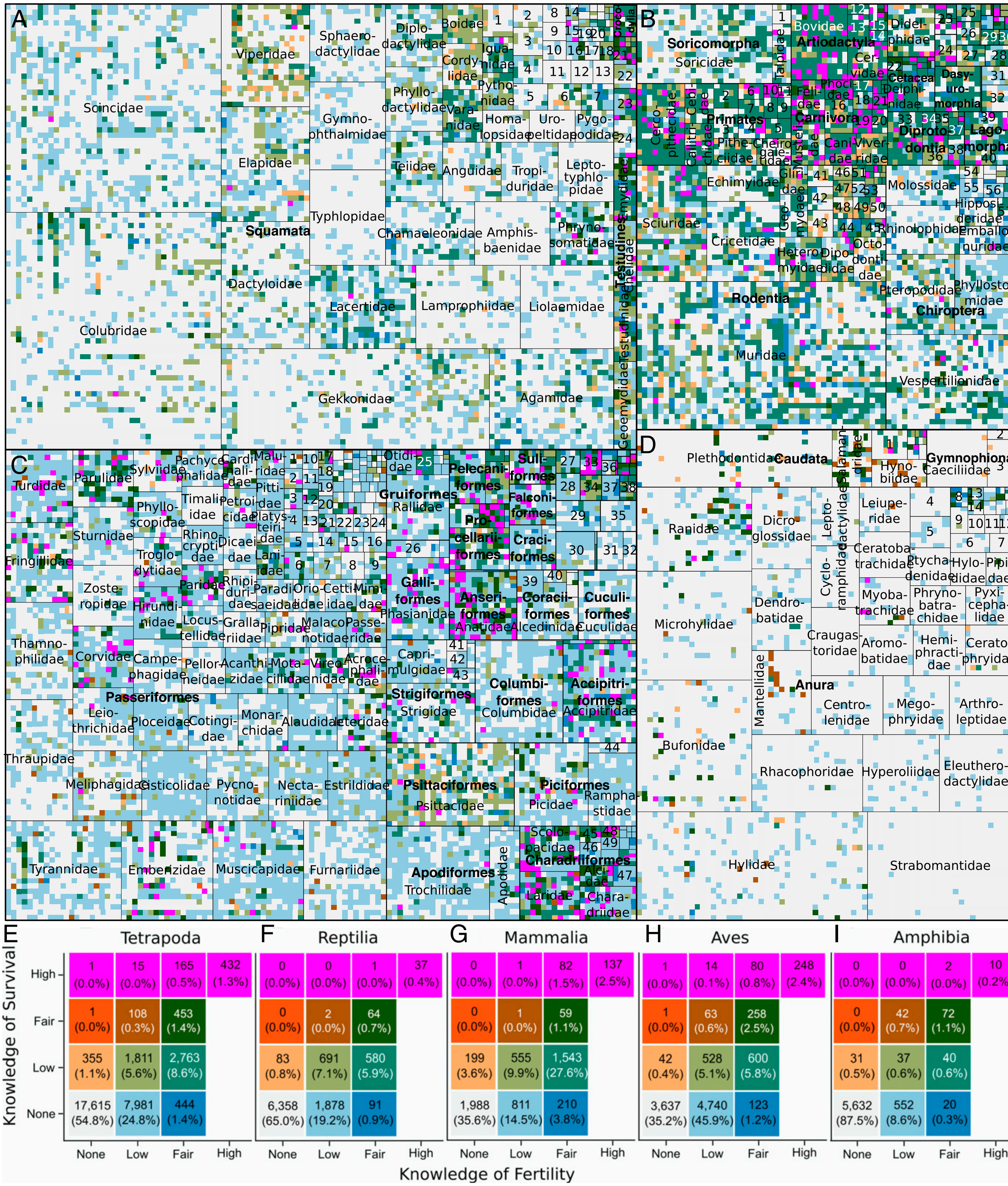

Fig. 1. Landscape of demographic knowledge for tetrapods. (*A*) Reptilia. (*B*) Mammalia. (*C*) Aves. (*D*) Amphibia. Each pixel represents a species, hierarchically ordered by families, orders, and classes. The level of information on fertility and survival is coded using a 2D color scale, with blue shades representing information on fertility and red shades representing information on survival. Green shades represent equal information on both. When only one measure was available, knowledge was classified as low. When two or more measures were available, knowledge was classified as fair. Knowledge was classified as high when detailed age-specific or stage-specific information was available in a life table or population matrix, indicated by the pink shade. Gray indicates no information. Squares show the number of species and percentages per index for all tetrapods (*E*) and divided by class (*F*–*I*).

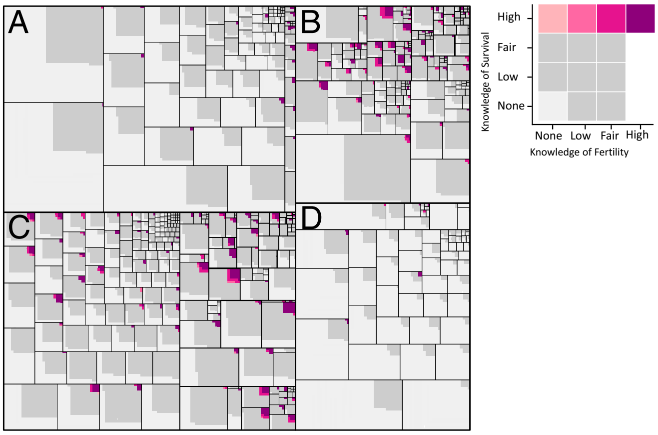

Fig. 2. Simplified version of the landscape shown in Fig. 1. (*A*) Reptilia. (*B*) Mammalia. (*C*) Aves. (*D*) Amphibia. Pink shades represent high knowledge of survival and various levels of knowledge about fertility. Dark gray shades represent low or fair knowledge, and the light gray areas indicate no demographic knowledge. For the entire range of tetrapods, only 1.3% of species have high survival and fertility information, less than 0.6% have high survival but little or no fertility information, 43.3% have limited survival and fertility information, and 54.8% have no survival or fertility information.

for Conservation of Nature Red List of Threatened Species (hereafter IUCN Red List) (11), which is the average age of mothers at the birth of offspring, and which provides a measure of the time required for a population to renew itself. Estimation of generation length ideally requires knowledge of age- or stage-specific survival and fertility. Likewise, to set up harvesting quotas, it is necessary to predict the impact of harvesting on the sustainability of a population. Therefore, population viability analyses are often required; these preferably use detailed measures of age- or stage-specific survival and fertility because these measures greatly improve estimation of population trends under different management scenarios and the prediction of extinction risk (12). For example, CITES, the Convention on International Trade in Endangered Species of Flora and Fauna usually requires these types of analyses for the establishment of exporting quotas for particular species to ensure that the international trade does not threaten the sustainability of their populations.

Detailed demographic data are essential not only for managing populations but also for understanding life histories and population dynamics. For example, age-specific mortality and fertility data are crucial for studies of the biology of aging in humans and nonhuman species (6, 7). Moreover, the patchy nature of the landscape of demographic knowledge is especially worrisome for threatened species for which data on closely related species are also lacking, as clearly illustrated by amphibians. After surviving four mass extinctions, amphibians now suffer the highest disappearance rate of all tetrapod classes (13). It is important that data gaps like these are filled by collection of field data, when possible; otherwise, data from captive populations can provide important information or estimates can be derived from closely related species.

Imputation methods are often used to fill information gaps when data on related species are available. These methods estimate missing data by using suites of trait correlations among species (14). For example, if detailed demographic measures are not available, simple life history traits, such as body size, have been used to make crude predictions of extinction risk. For highly data-deficient groups, a potential source of information lies in the availability of demographic and related measures from natural history museum collections, such as number of embryos in the uterus from preserved specimens, age estimates based on the characteristics of skulls or teeth, skeletal indicators of health, and size and weight of individuals at the time of capture. The incorporation of existing demographic data from unpublished studies, reports, and journals in languages other than English, as well as data from captive populations, will also play a key role in filling knowledge gaps.

To inform animal management decisions, zoos and aquariums collect detailed information on individuals under their care. For 45 y, Species360 has been gathering standardized information from institutions worldwide; currently, information is available for over 10 million individuals from 22,000 species (15). We found that the use of Species360 members' data could significantly increase knowledge, such as age at first reproduction from 4,199 species to 7,273 species, a 73% increase. More dramatically, the availability of life tables or population matrices could be increased from 613 species to 4,699 species, an almost eightfold gain.

Caution must be taken when using data from captive populations to model wild populations. Zoo and aquarium populations are intensively managed, and hence likely to differ from free-living populations, notably in survival (16) and reproduction metrics. Furthermore, we found that origin of the information for more than half of the species (66%) is unknown or not reported (Fig. 3 and *SI Appendix*, Table S3). Therefore, whether demographic measures were estimated from imputation analyses or from wild or captive populations is unclear (Fig. 3 and *SI Appendix*, Fig. S5). We found that between 75% and 85% of the species have an unknown or not reported origin of information for interlitter or interbirth interval, age at first reproduction, and litter or clutch size (Table 4). Likewise, 57% of the species have an unknown origin for maximum life span. This is worrisome because these data are widely used for conservation and comparative studies. Thus, gaining a better understanding of biases of data from unknown origin, imputation analyses, or populations under captive management should be a priority. In addition, it will be important to explore the uncertainty introduced by mixing data from wild and captive populations. In this sense, zoos, aquariums, and botanical gardens could become key allies in providing data that can help fill data gaps to understand species biology.

To address current biodiversity crises, key questions must be answered. Which species should be selected for long-term population

Table 2. Number of species per Demographic Species Knowledge Index and IUCN Red List categories

Demographic Species Knowledge Index		IUCN Red List category									
Survival	Fertility	LC	NT	VU	EN	CR	EW	EX	DD	NE	Total
None	None	6,609	977	1,220	1,331	771	5	132	2,484	4,086	17,615
None	Low	5,306	394	363	278	107	2	14	146	1,371	7,981
None	Fair	274	33	26	37	14	0	1	9	50	444
Low	None	169	20	39	19	13	1	2	26	66	355
Low	Low	1,031	105	117	89	37	0	8	51	373	1,811
Low	Fair	1,601	166	235	179	82	3	14	75	408	2,763
Fair	None	0	0	0	0	0	0	0	0	1	1
Fair	Low	69	8	9	7	2	0	0	2	11	108
Fair	Fair	305	31	31	20	8	0	0	0	58	453
High	None	1	0	0	0	0	0	0	0	0	1
High	Low	9	0	2	1	0	0	0	0	3	15
High	Fair	121	8	12	7	3	0	0	0	14	165
High	High	281	34	39	23	15	0	0	1	39	432
Total		15,776	1,776	2,093	1,991	1,052	11	171	2,794	6,480	32,144

CR, critically endangered; DD, data deficient; EN, endangered; EW, extinct in the wild; EX, extinct; IUCN, International Union for Conservation of Nature; LC, least concern; NE, not evaluated; NT, near threatened; VU, vulnerable. Further information about measures of knowledge for the Demographic Species Knowledge Index categories is provided in *Methods*.

Table 3. Total number of species per demographic measure or rate by taxonomic class

Demographic measure or rate	No. of species and percentage of species (%)			
Fertility	Reptilia	Mammalia	Aves	Amphibia
Age at first reproduction	758 (7.7)	1,977 (35.4)	1,279 (12.4)	199 (3.1)
Interlitter/interbirth interval	62 (0.6)	1,167 (21.0)	75 (0.7)	2 (0)
Litter/clutch size	3,340 (34.1)	3,364 (60.3)	6,652 (64.4)	711 (11.0)
Proportion of reproductive females	0 (0)	0 (0)	44 (0.4)	0 (0)
Recruitment	0 (0)	0 (0)	22 (0.2)	0 (0)
Age- or stage-specific fertility rates	37 (0.4)	137 (2.5)	248 (2.4)	10 (0.2)
Survival				
Maximum recorded life span	1,430 (14.6)	2,572 (46.0)	1,641 (15.9)	226 (3.5)
Mean age of (adult) population	0 (0)	0 (0)	0 (0)	114 (1.8)
Crude mortality	103 (1.1)	236 (4.2)	808 (7.9)	22 (0.3)
Age- or stage-specific death rate	38 (0.4)	220 (4.0)	343 (3.3)	12 (0.2)

The relative number of species per taxonomic class for which that measure exists is indicated in parentheses. Further information about measures of knowledge for the Demographic Species Knowledge Index is provided in *Methods*.

monitoring programs? How much effort should be devoted to digitization of existing records? How reliably can data from captive populations or imputation analyses fill demographic knowledge gaps? To use available resources more efficiently, prescription decision analyses will be necessary to prioritize data needs (4, 17). To achieve this goal, knowledge gaps in geographical, temporal, and taxonomic information must be addressed from field or zoo records or imputation analyses and, eventually, also from metrics of available genetic information. Although research and decision making now rely on large databases, financial support for data digitization, field data collection, and the integration of databases remains scarce.

Data, if grouped together, are greater than the sum of their parts. Imputation of fertility and mortality patterns becomes much more reliable if arrays of information are available for a species and for closely related species. Conservation action plans can be much more effectively targeted if based on multifaceted data. Initiatives such as the Darwin Core group by the Biodiversity Information Standards (TDWG) (18) are developing global data standards and uniform vocabularies on taxonomy, occurrence, and sampling events: This will facilitate the integration of biodiversity databases. Data on species interactions, physiology, genetics, and diseases remain among the most sought-after data types in biological research, conservation policy, and management practice. The publication of data through organizations such as the Global Biodiversity Information Facility can be used to facilitate integration of databases in the future. Creating linkages with research infrastructures like the Distributed System of Scientific Collections (19) will enable the integration of data to serve a broader audience of researchers and will enable new research. The Demographic Species Knowledge Index developed here serves as a first step toward a complete assessment of biodiversity knowledge across different disciplines for every species. We envision that our assessment of demographic knowledge for tetrapods lays the foundation for the development of a species knowledge index of digital information that identifies and classifies the amount and types of digital data available in knowledge areas such as genetics, primary biodiversity data, and species legislation, such as compiled by Legal Atlas (20) for all of our planet's described species.

We found that large regions of the landscape of demographic knowledge across tetrapods are less well known than the surface of Mars. Fuller knowledge will contribute not only to conservation biology but also to research on unifying concepts and fundamental relationships, shaped by evolution, across species. We show that data from captive populations can significantly increase our demographic knowledge.

Methods

Data Sources. To estimate the availability of demographic data for each of the 32,144 tetrapod species (97% of the extant described species), we developed a metadatabase using information contained in 22 published sources of demographic information (Table 1). We selected databases that contained machine-readable records and references to the original works. Also, we used databases for which data were freely available, although, in some cases, a memorandum of understanding was required before access was granted [e.g., for the Primate Life History Database (21)]. We excluded those records that were derived from imputation analysis when reported as such. We omitted databases for which data sources (i.e., references) could not be traced. Because of the low number of amphibians and reptiles represented in most databases, we conducted an online literature search for which we included all literature that had information on demographic data for at least 18 species.

Taxonomic and Terminology Standardization. We used TraitBank (22) as the reference for standardization of the terminology of demographic variables and rates across the 22 selected databases. However, for most, we could not find established standards; therefore, during an expert workshop with coauthors of this article, we developed an ontology that described eight demographic measures, as described below: five for fertility and three for survival.

We standardized species taxonomy across all of the databases using the Catalogue of Life's (9) currently accepted nomenclature. To retrieve the

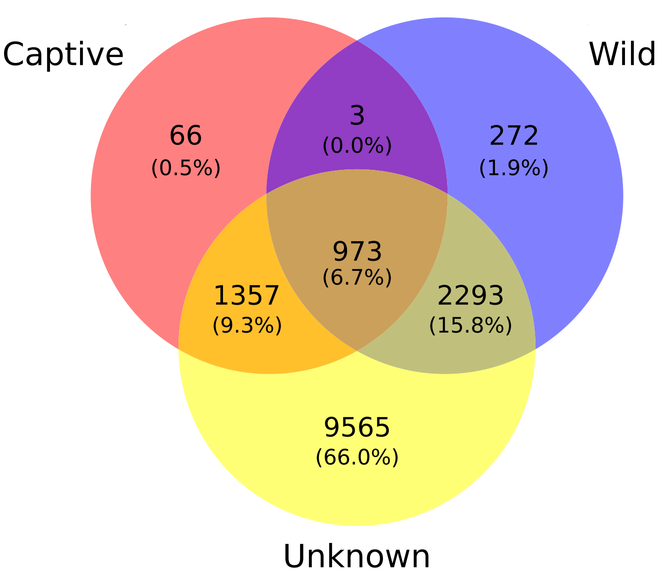

Fig. 3. Reported origin of the information across the 22 data repositories analyzed. Diagrams show all possible combinations of the number of species with data from populations from captive, wild, and unknown origins.

Table 4. Number of species indicating the origin (captive, wild, or/and unknown) from which demographic measures or rates were estimated for all tetrapods

Demographic measure	Origin/no. of species		
Fertility	Wild	Captive	Unknown
Age at first reproduction	1,222	43	4,114
Interlitter/interbirth interval	402	10	1,256
Litter/clutch size	2,413	31	13,735
Proportion of reproductive females	44	0	0
Recruitment	22	0	0
Age- or stage-specific fertility rates	416	14	22
Survival			
Maximum recorded life span	1,483	2,358	5,128
Mean age of (adult) population	0	0	114
Crude mortality	1,055	13	229
Age- or stage-specific death rate	580	48	26

A single species may have data from different origins.

accepted names and the IUCN Red List status (23), we used the taxize (24) package in R version 3.5.1 (25) and manually searched for species names that could not be retrieved. For 3% of the species, we were not able to resolve their taxonomy, so they were not included in the analyses. This process resulted in a metadatabase of 32,144 species, with 14,529 species with demographic data and 115,356 demographic records. We standardized each record's origin from populations reported as wild, captive, or unknown across all of the databases. When the origin was not provided in the database, we assigned it as "unknown" (Table 4); however, we still included those records because all of the databases included here have a reference to a publication.

Developing the Demographic Species Knowledge Index. To summarize the availability of demographic data for each tetrapod species we developed the Demographic Species Knowledge Index. This index provides scores that summarize the number of a total of eight measures available for fertility and survival for any species. These measures are as follows:

- Measures of fertility knowledge: (*i*) age at first reproduction; (*ii*) interlitter/interbirth interval; (*iii*) litter/clutch size; (*iv*) proportion of adult females that are reproductive; and (*v*) birth or recruitment rate, with recruitment denoting the average number of individuals that reach a specific age or stage (e.g., maturity, leaving the nest) per reproductive female.
- Measures of survival knowledge: (*i*) maximum recorded life span, (*ii*) mean age of the (adult) population, and (*iii*) crude mortality. Information about mortality (or survival) includes the juvenile crude death rate, the adult crude death rate (or adult life expectancy, approximately the inverse of the adult crude death rate), and the crude death rate for juveniles and adults combined (or life expectancy at birth, which is approximately its inverse). The crude death rate is given by the number of deaths in some time interval over average population size in the interval. The probability of death equals the number of deaths in some time interval divided by population size at the beginning of the interval. Biologists sometimes refer to one minus either of these measures as the survival rate.
- Combined age or stage survival-fertility knowledge: The index is also based on the availability of population-level data in the form of population matrices or life tables. These include both age- or stage-specific death or survival probabilities and age- or stage-specific fertility rates; life tables often contain only mortality data.

Knowledge about survival is classified into four categories:

- High: A life table or population matrix is available.
- Fair: Such data are not available, but at least two variables are measured, such as maximum life span and adult mortality.
- Low: Only one variable is available.
- None: No information is available.

Knowledge about fertility is also classified into four categories.

- High: Fertility rates are available by age or stage.
- Fair: Such data are not available, but at least two variables are measured, such as age at maturity and average litter/clutch size.
- Low: Only one variable is available.
- None: No information is available.

Life tables and matrices always contain survival information but do not always have information on fertility, which is usually harder to obtain in the wild. Hence, in Fig. 1, only 13 categories are color-coded. The metadatabase to estimate the index and the index are both available in the Species360 Open Data Portal and Dryad Digital Repository (48, 49).

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